ON THE FORE LIMB OF ALLOSAURUS FRAGILIS.

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In unpacking, recently, that part of the Marsh collection in the United States National Museum from near Canon City, Colorado, a partial skeleton of a carnivorous dinosaur was found. This is of peculiar interest since it has been determined to belong to the same individual as the pelvis and hind limbs described and figured 1 by Prof. O. C. Marsh, years ago, as Allosaurus fragilis. Both fore limbs and feet are present, and as they differ materially from the fore limb figured by Marsh in the paper cited above, and especially since an associated fore limb of this genus has not previously been known, it was considered important that a description (of the limb and foot) should be published in advance of the remainder of the skeleton, which is now undergoing preparation, a work that will take some time to complete.

The fore limb figured by Marsh in the Dinosaurs of North America,² plate 11, figure 1, as being that of *Allosaurus fragilis* Marsh, is a composite drawing, and, as I will show, is not representative of the

genus Allosaurus, but is largely that of Ceratosaurus.

In going over a lot of tracings and drawings of Theropodous dinosaur bones made for Professor Marsh, a slip of paper in Marsh's handwriting was found, on which he had written instructions to the draftsman for the composition of the *Allosaurus* fore limb (fig. 1), which reads as follows:

Fore limb Allosaurus.

1. Enlarge scapula (1933 as 83.5 is to 100).

2. Make coracoid to correspond (see Phillips, p. 208).

3. Draw humerus (1894 nat. size).

4. Make radius 9½ inches long.
5. Make ulna 9½ inches long + olecranon.

6. Enlarge foot as 83.5 is to 100.

The number 1933 is the catalogue number of the Peabody Museum originally given to the type-specimen of *Ceratosaurus nasicornis* Marsh before its transfer to the United States National Museum.

¹ Amer. Journ. Sci., vol. 27, 1884, p. 336, pl. 11.

² Sixteenth Ann. Rep. U. S. Geol. Surv., 1896, pt. 1.

The coracoid, which is not present with the *Ceratosaurus* skeleton, was evidently modified from a figure of that bone in Phillips Geology. The humerus is from another specimen and the radius, ulna, and foot were evidently drawn from those bones pertaining to the type-specimen of *Ceratosaurus nasicornis* Marsh.

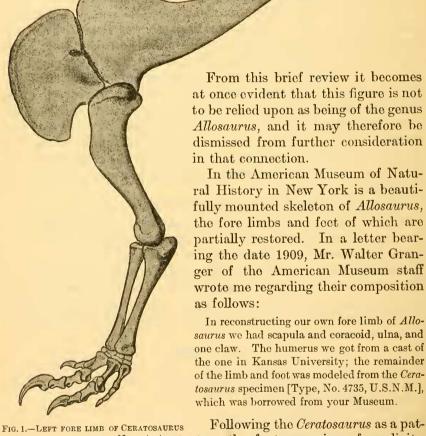


Fig. 1.—Left fore Limb of Ceratosaurus (Allosaurus fragilis of Marsh). After Marsh.

Following the *Ceratosaurus* as a pattern the foot was given four digits, whereas the specimen before me shows

quite conclusively that *Allosaurus* had but three digits, with a reduced mtc. III. The phalangial formula in the New York specimen is correct, and the relative proportions of the various segments of the limbs are entirely in accord with the associated material forming the basis of the present paper. In view of the limited fore limb and foot material available at the time of reconstructing this limb and foot of *Allosaurus*,

those in charge of that work are to be congratulated upon their close approximation to the facts as revealed by the discovery of this more recent material.

Remove the fourth digit, replace mtc. III by mtc. IV and insert the carpal bones and the limb would be quite in accord with the fossil specimen before me.

Hay ¹ in 1908 in commenting upon the New York specimen concluded that it had been wrongly identified as *Allosaurus*, because of the great size of the hand in relation to the other segments of the limb, being led into this mistaken idea by relying upon the then supposed authentic figure of the limb and foot as published by Marsh.

Williston² in 1902 in describing some limb material secured by him in Wyoming refers to the so-called *Allosaurus* fore limb figured by Marsh in the following:

There were two scapulae obtained that certainly show a generic distinction from *Allosaurus*, as I have convinced myself from inspection of the scapula referred by Marsh to that genus, and figured by him in various places. It remains to be seen, however, whether this scapula of Marsh indubitably belongs with the bones first referred by him to *Allosaurus*. I do not think there is conclusive evidence of this.

The facts regarding this scapula as presented on a preceding page bears out Dr. S. W. Williston's conclusion.

The type of Allosaurus fragilis Marsh is in the Peabody Museum of Yale University, and in a recent letter Dr. R. S. Lull informs me that it consists of two vertebrae and one phalange, from Garden Park, Canon City, Colorado, collected by B. F. Mudge in 1877. It bears the catalogue number 1930. The type material is from the same locality as the specimen described here and possibly from the same quarry. The fore and hind limbs figured so widely by Marsh do not pertain to the type-specimen, although such reference ³ has been made regarding them.

FORE LIMB AND FOOT.

The fore limb of *Allosaurus* as compared with the hinder is relatively small, but the large size of the processes and the rough nature of their surfaces imply a powerful musculature. The great size of the terminal phalanges and the general structure of the foot indicates that it was used exclusively for seizing, holding, and tearing, and that it had long ago lost its function as an organ of progression. The hand is relatively of enormous size, being slightly longer than the humerus and nearly one and one-half times as long as the forearm. In general it resembles the foot of *Ornitholestes*, although the bones are more robust, and there is no trace with either foot of mtc. IV.

The carpus is ossified, there being two transverse rows, but the precise number of elements composing it yet remains to be determined.

¹ Proc. U. S. Nat. Mus., vol. 35, 1908, p. 355.

² Amer. Jour. Sci., vol. 11, 1901, p. 112.

⁸ O. P. Hay, Proc. U. S. Nat. Mus., vol. 35, 1908, p. 355.

There are three digits, which have the phalangial formula of 2, 3, and 4. Digit one is the heaviest of the series and mtc. III is reduced. Scapula.—Both scapulae are preserved with the present specimen,

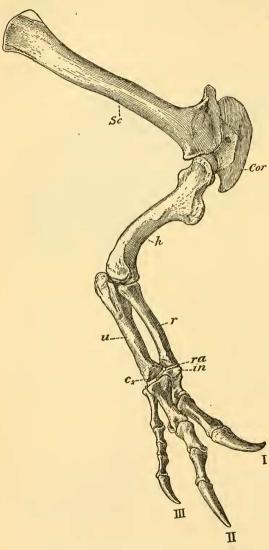


FIG. 2.—RIGHT FORE LIMB AND FOOT OF ALLOSAURUS FRAGILIS MARSH. CAT. NO. 4734, U.S.N.M. § NAT. SIZE. LATERAL VIEW, C₂, CARPALE TWO; Cor, CORACOID; h, HUMERUS; in, INTERMEDIUM; r, RADIUS; ra, RADIALE; Sc, SCAPULA; u, ULNA; I, II, AND III, DIGITS ONE, TWO, AND THREE. THE POSITION OF THE MISSING ULNARE IS INDICATED BY DOTTED LINES.

the right being perfect, as shown in figure 2, with the exception of a small portion of the upper anterior corner of the blade which is missing. left scapula was injured in life and the subsequent healing produced great deformation of the bone. This pathologic condition caused a widening of the blade that would be entirely misleading as to its true form had not the opposite scapula been present. The scapula of Allosaurus is distinctive on account of its bird-likeform, as has previously been pointed out by Williston.1 The shaft is exceptionally long and slender, being nearly of equal width throughout except the uppermost or distal extremity, which is perceptibly widened. This expansion is about equal in fore and aft direction. The upper third is flattened and thin, while more proximally the shaft is trihedral in cross-section, the anterior border being sharp, the posterior one rounded. Longitudinally the external surface

is convex, though nearly straight in its middle portion, a shape that probably conformed closely with the convex curve of the body cavity.

The inner surface of the greater part of the blade is flattened anteroposteriorly while the outer surface, excepting the upper fourth, is rounded in this direction. The articular end being expanded both antero-posteriorly and transversely is heavy, especially on the posterior half, which has a maximum thickness immediately above the glenoid fossa of 58 mm. The scapula unites with the coracoid by a straight suture that bisects the glenoid fossa and is terminated above by a deep notch between the scapula and coracoid on the anterior border. In this individual both scapulae are firmly coossified with their respective coracoids. The scapula of this specimen appears to agree in all particulars with the one found with the mounted skeleton of Allosaurus in the American Museum of Natural History, and it also shows that the limb described by Williston should be referred to this genus.1 In this connection it is of interest to know that the Ceratosaurus scapula which formed the basis for the illustration of this bone in the so-called fore limb of Allosaurus is now in the United States National Museum collections (fig. 1). I have recently examined the bone and find that its upper extremity is incomplete, so that it is not positively known whether this blade has a nonexpanded end as represented by Marsh or whether it was expanded as in Allosaurus. It differs, however, from Allosaurus in having a thinner and wider shaft and a more abrupt backward curve of the heavy posterior border just above the glenoid fossa. Both inner and outer surfaces of the lower three-fourths of the shaft in Allosaurus are rounded. Both of these specimens came from the famous quarry No. 1 near Canon City. Fremont County, Colorado,

Measurements of scapula.

Greatest length of right scapula and coracoid, measured along outside curve	mm. 795
Greatest length of right scapula. Greatest breadth of right scapula.	$652 \\ 175$
Greatest breadth of blade, upper end	² 145
Least breadth of blade Greatest expanse of glenoid fossa	

Coracoid.—The coracoid in Allosaurus is quadrangular in outline, the infero-superior measurement exceeding the antero-posterior diameter. The outer surface is convex in all directions, the inner decidedly concave antero-posteriorly. There is a broad notch on the inferior border.

The coracoid is pierced by the usual foramen, which runs diagonally through the bone, the external exit being larger than the inter-This foramen is entirely inclosed (fig. 2), not a notch as shown in Marsh's figure of the coracoid (fig. 1). The superior border presents a thin flattened edge, the anterior edge gradually thickening toward the inferior border.

Measurements of coracoid.

	mm
Greatest length at center	120
Greatest depth at center	170

Humerus.—Comparatively the humerus of Allosaurus is short and somewhat sigmoid in form. The shaft is hollow, as are all of the limb and foot bones of this genus. Planes passed through the

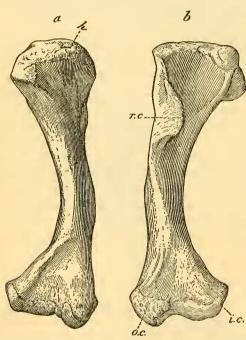


Fig. 3.—Right humerus of Allosaurus fragilis Marsii. Cat. No. 4734, U.S.N.M. $\frac{1}{4}$ nat. size. a, back view; b, front view; b, head; τ , c., radial crest; i. c., inner condyle; o. c., outer condyle.

greatest diameters of the articular ends would cut one another at an angle of 50°. This unusual angulation throws the articulated radius and ulna well out away from the body. The deltoid or radial crest is strongly developed as a short but high thin plate of bone, that is situated on the anterior-external border immediately above the middle of the shaft. Viewed from the front it renders the anterior surface deeply concave transversely (fig. 3). Below this crest the shaft is constricted and angularly rounded in crosssection. The head is situated in about the middle of the proximal end with the articular portion overhanging the posterior sur-

face of the shaft. The radial and ulnar condyles are well defined. Posteriorly they are separated by an unusually broad but shallow depression which continues somewhat upward on the shaft of the bone. The articular ends of the humerus are rugosely roughened. A prominent roughened oval-shaped area on the posterior-external surface at the lower border of the radial crest probably represents the point of insertion for the humero-radialis muscle (fig. 2). The measurements given below were made from the humerus of the right side, which is the better preserved of the two:

Measurements of humerus.	mm.
Greatest length	310
Greatest width of proximal end	118
Greatest width of distal end	
Least diameter of shaft	38

Ulna.—The ulna is expanded and heavy proximally with a less expanded distal end. It exceeds the radius in length but is shorter than the humerus. The proportion being as 1::1.17.

There is a heavy olecranon process (o, fig. 4) that extends considerably above the articular surface for the humerus. The surface of this process is roughened for muscular insertion. The olecranon



FIG. 4.-LEFT ULNA OF ALLOS-AURUS FRAGILIS MARSH. CAT. No. 4734, U.S.N.M. 1 NAT. SIZE. POSTERIOR VIEW.

process is less well developed in Ceratosaurus nasicornis and appears to be entirely wanting on the ulna of Ornitholestes hermani.

The articular surface for the humerus is comparatively narrow transversely, with a shallow concave surface anteroposteriorly. The concavity on the proximal end for the reception of the head of the radius is shallow. The shaft of the ulna is slender, suboval in cross-section, and in a distal direction, grad-



FIG. 5.—RIGHT RADIUS OF ALLO-SAURUS FRAGILIS MARSH. CAT. No. 4734, U.S.N.M. 1 NAT. SIZE. INTERNAL VIEW. d, DISTAL END; p, PROXIMAL END.

ually expanding into a moderately large end, the greatest diameter being antero-posterior. The distal end is oblique to the longer axis of the bone, the surface of which looks downward and forward in the articulated limb. On the inner anterior face of the distal end a prominent roughened protuberance presents a surface for union with the radius.

Measurements of ulna.	mm.
Greatest length	263
Greatest diameter of proximal end	
Greatest diameter of distal end.	
Least diameter of shaft	

Radius.—The radius is more slender and somewhat shorter than the The proximal and distal ends are expanded, more especially the former (fig. 5). In cross-section the shaft is angularly rounded throughout the greater part of its length. The proximal end is shallowly concave in its greatest diameter. Viewed from above this end is suboval in outline. The distal end is subtriangular in outline, with an oblique surface that looks downward and outward. It articulates exclusively with the radiale of the carpus. The inner surface where the radius meets the ulna is slightly roughened.

Measurements of radius.	mm.
Greatest length	222
Greatest diameter of proximal end.	
Greatest diameter of distal end	40
Least diameter of shaft	

Carpus.—The ossified carpus in Allosaurus consists of at least five elements, with a possibility of there being one more. Three disarticulated elements were found with the bones of the left foot and three with the right, but since there is an element with each foot that is not present in the other, and the ulnare is lacking in both, the presence in the complete carpus of five ossified carpals is quite conclusively demonstrated. Fortunately two of those pertaining to the right foot (fig. 7, in and c_2), the intermedium and a carpale, probably c_2 , were

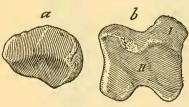


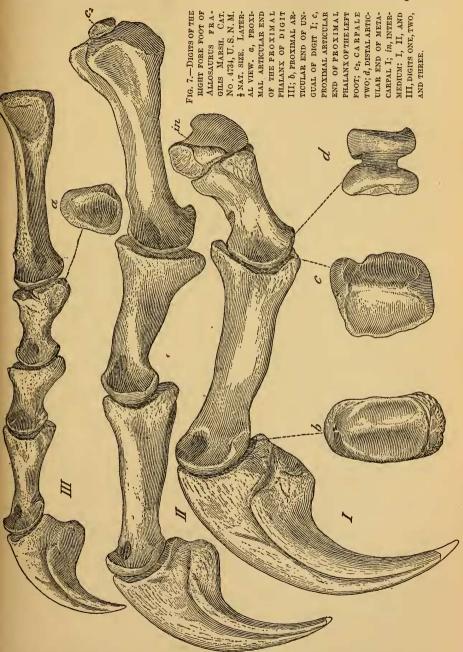
Fig. 6.—Carpal bones of allosaurus fragilis Marsh. Cat. No. 4734, U.S.N.M. $\frac{1}{2}$ nat. Size. Viewed distally. a, radiale of the right fore foot; b, intermedium of the left fore foot; II, surface articulating with metacarpal II, I, surface articulating with metacarpal II.

found in position, firmly attached to metacarpals I and II, and these give the first definite knowledge we have of the exact manner of their articulation. Without such evidence it would be almost impossible to place them properly. I was also able to determine the proper articulation of the radiale by its position as found in the matrix and also by its close articulation with the grooved surface of the intermedium.

The radiale is a flattened discoidal element, irregularly oval in outline (fig. 6a). The upper articular surface is shallowly concave while the distal surface is angularly convex. This surface in the articulated foot articulates for more than half its area with the intermedium and slightly if at all with the inner posterior corner of mtc. I. Its greatest transverse diameter is 41 mm.; greatest thickness, 15 mm.

The intermedium as shown in figure 6b, is an irregularly quadrangular bone. Articulated it rests about equally upon the proximal ends of mtcs. I and II (fig. 2, in and ra). The upper surface presents a broadly grooved surface for the radiale (fig. 7), with a projecting spur on the anterior face that continues to the outer border of mtc. I, so that when viewed from the front it appears to completely cover the metacarpal. On the pos'erior external side a somewhat similar projection overlaps a beveled surface on the outer proximal end of

mtc. II. The outer end of this projection is separated by a notch from a smaller process on the anterior border that also rests upon a



beveled articular facet on the end of mtc. II. The intermedium has a greatest transverse diameter of 51 mm.; greatest antero-posterior diameter is 40 mm.

The ulnare is not known. Carpale two is apparently represented by the small flattened ossicle that was found attached to the proximal end of mtc. II (fig. 7c), of the right foot which is in close apposition to the outer anterior border of the intermedium. A detached bone found near the left manus is regarded doubtfully as representing c_3 . It is elongated in one diameter with angularly rounded surfaces. There is no clue as to the position it occupied on the foot, if indeed it represents such an element. Its longest diameter is 31 mm., with a least diameter of 11 mm.

Metacarpus.—The complete metacarpus in Allosaurus apparently consists of three elements, there being no trace in either foot, of mtc. IV which is present in the manus ¹ of Ornitholestes hermani Osborn.

Mtc. I is a short heavy bone with a deeply grooved distal end that is turned inward away from the central axis of the foot. The articular facets extend well upward on both front and back aspects (fig. 7d), rising about equally above these surfaces of the shaft. The lateral pits are moderately shallow, the outer one being the better defined. Viewed from above the proximal end is subtriangular in outline with a shallow concave articular end. This surface is opposed in the articulated foot by the radiale and intermedium, the former only touching slightly the hinder internal corner, the remaining surface being closely applied to the intermedium, as shown in the right foot, where these bones were found articulated. Mtc. I articulates closely on its upper half with mtc. II (fig. 2), resting in a broad shallow depression on the side of that bone. Mtc. II is an elongate bone, having an expanded subquadrangular proximal end, rather a slender, angular rounded shaft, and a less expanded but broadly grooved distal extremity. The articular surfaces of the distal end of this bone are continued backward in the form of two lateral condylar-like facets, which are separated by a deep and moderately broad notch. The external one is the larger of the two. The inner border of the proximal end is beveled off, forming two facets of unequal size for the articulation of the intermedium. The remaining proximal surface is smooth though sloping toward the outside of the foot. Mtc. III is reduced, being the weakest element of the metacarpus. Although present with both feet, it was detached in both instances. The character of the surfaces appears to indicate, however, that in position it has a weak articulation with mtc. II on the postero-external angle as shown in figure 2. Unlike the other metacarpals, the distal articular end is not grooved but is smoothly rounded (fig. 7a). posteriorly directed facets are weakly developed, but are separated by a shallow groove as in mtcs. I and II.

Phalanges.—The phalangial formula is 2, 3, 4. All of the digits, as shown in figure 7, are terminated with latterly compressed, sharply

pointed claws, the first being especially robust, the third much reduced in size. The proximal phalanx of digit one is the longest of the series. The proximal articular surface is concave superoinferiorly, with a strongly developed vertical keel which articulates with the deep groove on the distal end of mtc. I. This keel as shown in figure 7c, divides this articular end into two unequal concave surfaces, the larger one being toward the outer side of the foot. It is inclined to the vertical axis of the bone and when articulated rotates the distal end so that the ungual phalanx is turned inward from the vertical as shown in figure 2. The articular surface for the claw is broadly grooved, and this surface extends well backward on the under side, thus throwing the articulated ungual downward at nearly a right angle to the longer axis of the first phalanx. The lateral pits are comparatively shallow, the one on the external side being the better defined. Viewed from above the shaft is quite evenly rounded transversely, while the ventral surface presents a flattened aspect. The ungual of digit one is especially robust, with a regularly curved and sharply pointed extremity. Well-defined lateral grooves run back from the tip on both sides, but as they approach the proximal end curve downward, passing into a broad smooth surface on the posterior ventral surface. proximal articular surface is keeled as shown in figure 7b.

The proximal phalanx of digit two is shorter than the second of that The proximal end of the former is expanded especially in the vertical direction. The proximal end as compared with the same phalanx of digit one is only slightly concave supero-inferiorly with a comparatively low obtuse keel, placed more toward the inside of this end. Like the keel on the proximal phalanx of digit one it is placed at an angle to the vertical axis of the bone. The concave lateral depressions on either side near the distal extremity are so shallow and illy defined they could hardly be designated as pits. The second phalanx of this digit is slightly longer than the first, with a sharply keeled proximal end and broadly grooved distal articulating surface. The lateral pits are small but well defined. The ungual phalanx is intermediate in size between those of the first and third toes.

The proximal phalanx of digit three can be distinguished from all others in the foot by the keelless, but cupped articular surface of the proximal end (fig. 7a). It is relatively short, as is the second, the third being more elongate. The proximal ends of the other phalanges of this toe are keeled, and the distal ends are grooved. The ungual except for its small size is very similar to the ungual of digit two. These two unguals are distinguishable from the ungual of digit one, not only by difference in size but also by the change in direction of the heavy portion below the articulating surface. In the two former in the articulated foot it looks almost directly backward, whereas in the first it is directed downward and backward. A comparison of this foot with the manus recently described by Lambe ¹ leads me to believe that the digit designated by him as the second is really the first. This is indicated by the shortness of mct. I, and especially by the phalangial formula. In all associated fore feet of Theropodous dinosaurs as shown in the accompanying table, there are two phalanges on the first digit with a progressive increase to the point where some of the lateral toes have commenced to degenerate. The lengthening of the penultimate phalanges appears peculiar to Theropodous dinosaurs and is a mechanical development for the more perfect use of the talons of the fore feet. The principal measurements of the bones of the manus are shown in the following table:

MEASUREMENTS OF FORE-FOOT ELEMENTS.

Meta carpals.

	1	Ι.	I	ſ.	III.		
	R.	L.	R.	L.	R.	L.	
Greatest length	mm. 73 35 36 35	mm.	mm. 125 56 46 22	mm. 122 63 46 22	mm. 105 29 23 11	mm. 97 28 22 10	

Phalanges.

Greatest length first row phalanges	118	138 120	94 102	94	50 41	42 43
Greatest length third row phalanges			95		52 61	55 59

PHALANGIAL FORMULAE OF VARIOUS THEROPODS.

Names		I	Digit	s.		Formation,	Remarks.		
Names.	I.	II.	III.	IV.	v.	Formation.	wemarks.		
Gorgosaurus libratus Lambe	0	2	3	0	0	Belly River, Up- per Cretaceous.	Skeleton in Ottawa Museum, Canada.		
Ceratosaurus nasicornis Marsh	2	3	3	1	0	Morrison, Upper Jurassic.	Mounted skeleton in U.S.N.M., Cat. No. 4735. Marsh's fig. D. of N. A. (Allosaurus fragilis).		
Ornitholestes hermani Osborn	2	3	4	0	0	do	Mounted skeleton in A. M. N. H., No. 587.		
Allosaurus fragilis Marsh	2	3	4	1	0	Morrison	Mounted skeleton in A. M.		
Do	2	3	4	0	0	Morrison, Upper Jurassic.	Skeleton in U.S.N.M., No.		
Hallopus victor Marsh	2	3	4	3	0	Upper Jurassic	Evidence for formula un- known. Specimen in Yale University.		
${\it Compsognathus longipes} {\it Wagner.}$	2	3	3	0	0	do	From Marsh's restoration of the skeleton.		
Anchisaurus polyzeius Marsh	2	3	4	2	1	Triassic	Formula that of restoration by Marsh. in D. N. Am. Skeleton in Yale Museum.		
Anchisaurus colurus Marsh	2	3	4	3	1	do	Skeleton in Yale Museum.		

¹ The Ottawa Naturalist, vol. 27, 1914, pp. 219-131, pl. 13.

The more important progressive changes that have taken place in the specialization of the fore limb and foot in the carnivorous dinosauria during successive geological periods now appear to be, (1) a reduction in the number of digits; (2) the elongation of the penultimate phalanges; (3) a lengthening of the scapula; (4) the shortening of the fore arm; (5) a relative reduction in size of the entire fore limb.

With the exception of Ceratosaurus, which has both inner and outer fingers reduced, all of the other known carnivores show that the reduction in the number of digits takes place on the outside of the foot. Beginning with the oldest known Theropods from the Triassic, all are found to possess the full complement of five digits, though the fifth is often rudimentary. In the Jurassic we find in Ornitholestes that the fifth digit has entirely disappeared, and the fourth is only represented by a vestigal metacarpal. Allosaurus appears to have gone still further and apparently the fourth has been lost and the third is somewhat reduced, and approximately the same condition obtains in the hand of Comsognathus from the Upper Jurassic of Bavaria.

Our knowledge of the manus in the Cretaceous Theropodous dinosaurs is rather meager at this time, but a specimen recently described by Lambe ¹ (Gorgosaurus libratus) from the Upper Cretaceous (Belly River) shows a still further reduction, there being only two functional digits, the third (fourth of Lambe) being represented by the vestigal metacarpal only.

¹ Ottawa Naturalist, vol. 28, 1914, pp. 13-17.